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Phenacomys intermedius. By James A. McAllister and Robert S. Hoffmann

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Phenacomys Merriam, 1889

Phenacomys Merriam, 1889:28. Type species, *Phenacomys intermedius* Merriam. Genus *Phenacomys* (including *Arborimus* Taylor, 1915) contains three species.

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Arvicolineae, Tribe Microtini (Carleton and Musser, 1984; Gromov and Polyakov, 1977). A key to the genus follows:

- | | | |
|------|---|-------------------------------|
| 1 | Tail short, less than 42 mm | <i>Phenacomys intermedius</i> |
| | Tail long, more than 50 mm | 2 |
| 2(1) | Tail thin, sparsely haired, 62 to 71 mm; upper incisors not strongly recurved; lateral pterygoid fossae deep | <i>Phenacomys albipes</i> |
| | Tail somewhat thickened, well haired, 60 to 83 mm; upper incisors strongly recurved; lateral pterygoid fossae shallow | <i>Phenacomys longicaudus</i> |

Phenacomys intermedius Merriam, 1889

Heather Vole

Phenacomys intermedius Merriam, 1889:32. Type locality "a basaltic plateau about 20 miles NNW of Kamloops," 5,500 ft, British Columbia.

Phenacomys celatus Merriam, 1889:33. Type locality "Godbout, P.Q." [=Quebec].

Phenacomys latimanus Merriam, 1889:34. Type locality "Fort Chimo, Ungava, Hudson Bay" [=Quebec].

Phenacomys ungava Merriam, 1889:35. Type locality "Fort Chimo, Ungava, Hudson Bay Territory" [=Quebec].

Phenacomys orophilus Merriam 1891:66. Type locality "Salmon River [=Lemhi] Mountains, Idaho (near head of Timber Creek)."

Phenacomys truei J. A. Allen, 1894:331. Type locality "Black Hills" [=Laramie Mountains], Wyoming.

Phenacomys oramontis Rhoads, 1895:941. Type locality "Church [Libumiton] Mountain, British Columbia."

Phenacomys preblei Merriam, 1897:45. Type locality "Twin or 'Lilies' Peak, near Longs Peak," Colorado.

Phenacomys olympicus Elliot, 1899:225. Type locality "Happy Lake, Olympic Mountains, Clallam Co., Washington."

Phenacomys constablei J. A. Allen, 1899:4. Type locality "Telegraph Creek, British Columbia."

Phenacomys mackenzii Preble, 1902:182. Type locality "Fort Smith, Slave River (near Athabasca-Mackenzie boundary line)."

Voorhies (1984) also referred *Propriophenacomys uptergovernensis* Martin, 1975, to *Phenacomys intermedius*.

CONTEXT AND CONTENT. Context in generic summary above; nine subspecies of *P. intermedius* recognized by Hall (1981) as follows:

P. i. celsus Howell, 1923:158. Type locality "Muir Meadow at 9300 feet, Tuolumne Meadows, Yosemite National Park, California."

P. i. crassus Bangs, 1900:39. Type locality Rigolet, Hamilton Inlet, Labrador.

P. i. intermedius Merriam, 1889:32, see above (*constablei* J. A. Allen, *orophilus* Merriam, *preblei* Merriam, and *truei* J. A. Allen are synonyms).

P. i. laingi Anderson, 1942:59. Type locality "Kimsquit River, Cornice Creek, near head Dean Inlet, latitude about 52°54' north, longitude about 127° west, altitude 2500 feet" British Columbia.

P. i. levis Howell, 1923:157. Type locality "Saint Mary's Lake, Teton County, Montana."

P. i. mackenzii Preble, 1902:182, see above.

P. i. oramontis Rhoads, 1895:941, see above (*olympicus* Elliot and "*Microtus (Lagurus) pumilis*" Elliot are synonyms).

P. i. soperi Anderson, 1942:58. Type locality "Swanson Creek, in the middle of Section 34, Township 19, Range 17, Riding Mountain National Park, Manitoba, about ten miles east of Park Headquarters at Wasagaming, on Clear Lake, altitude 2016 feet."

P. i. ungava Merriam, 1889:35, see above (*celatus* Merriam and *latimanus* Merriam are synonyms; see Remarks).

DIAGNOSIS. Characters in this section are taken mainly from Howell (1926); others are from Anderson (1942), Hinton (1926) and Peterson (1966). Unique enamel pattern of molars; re-entrant angle of mandibular teeth deep lingually (angles extend more than halfway across the molar), buccal angles shallower (Fig. 1). Palate not continuous transversely and shelf-like as in *Clethrionomys*, but possessing a broad bony "bridge" between lateral and median palatal projections that mostly cover the lateral palatal grooves (Fig. 1). Lateral pterygoid fossae shallow. Rooted molars lacking cementum in re-entrant angles in adult. White or pale gray feet in nonmolting specimens. Tail less than 50 mm (less than one-half body length), sharply bicolored. Stiff orange hair in ears (Johnson, 1967).

GENERAL CHARACTERS. *Phenacomys intermedius* is a small, short-tailed rodent (Fig. 2) that externally resembles the montane vole (*Microtus montanus*), with which it is widely sympatric; differentiating characters are mainly dental. The external resemblance is so close that Merriam (1889) chose the name "deceiver mouse" for the genus. Dorsal pelage agouti gray to brownish (some subspecies yellowish); ventral pelage whitish to grayish. The forefoot has five plantar pads whereas the hind foot has six; the lateralmost pad on the hind foot is the largest. The posterior half of the sole of the hind foot is well haired. Facial vibrissae reach the shoulders. There are eight mammae, two pectoral and two inguinal pairs (Howell, 1926), or two pectoral, one postabdominal and one inguinal pair (Harper, 1961). The adult skull has prominent lateral ridges in dorsal view, and distinct supraorbital ridges border a medial longitudinal frontal sulcus (Fig. 1). The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16. The first lower molar is notable for its variability in number of closed triangles, from three to seven (Hinton, 1926; Howell, 1926). The ascending ramus of the jaw is long; the articular facet is slightly above the level of the coronoid process (Fig. 1). The base of the lower incisor ends posterolateral to the alveolus of the last molar.

Johnson (1973) contrasted the genus *Phenacomys* (sensu stricto) with the included subgenus *Arborimus* for the purpose of elevating *Arborimus* to full generic rank, and listed many characters. *Phenacomys* (sensu stricto) possesses hip glands, 22 to 25 Meibomian glands (on upper and lower eyelids), and robust, often branched, cecal villae (Voge and Bern, 1949).

DISTRIBUTION. Howell (1926) described the range of *P. intermedius* as encompassing boreal areas (Canadian and Hudsonian zones) of Canada, and on the boreal summits of the Rocky Mountains, the Sierra Nevadas, and the mountains in the Great Basin (Fig. 3). It does not extend further south than the mouth of the St. Lawrence River or the Great Lakes in eastern Canada. The southwestern distribution corresponds to suitable habitat in the montane taiga (coniferous forest) biome occurring at progressively higher elevations in the north-south trending mountain ranges. Some southern montane populations probably are isolated, even though most published maps show the range to be continuous (Hall, 1981). Hagmeier (1966)

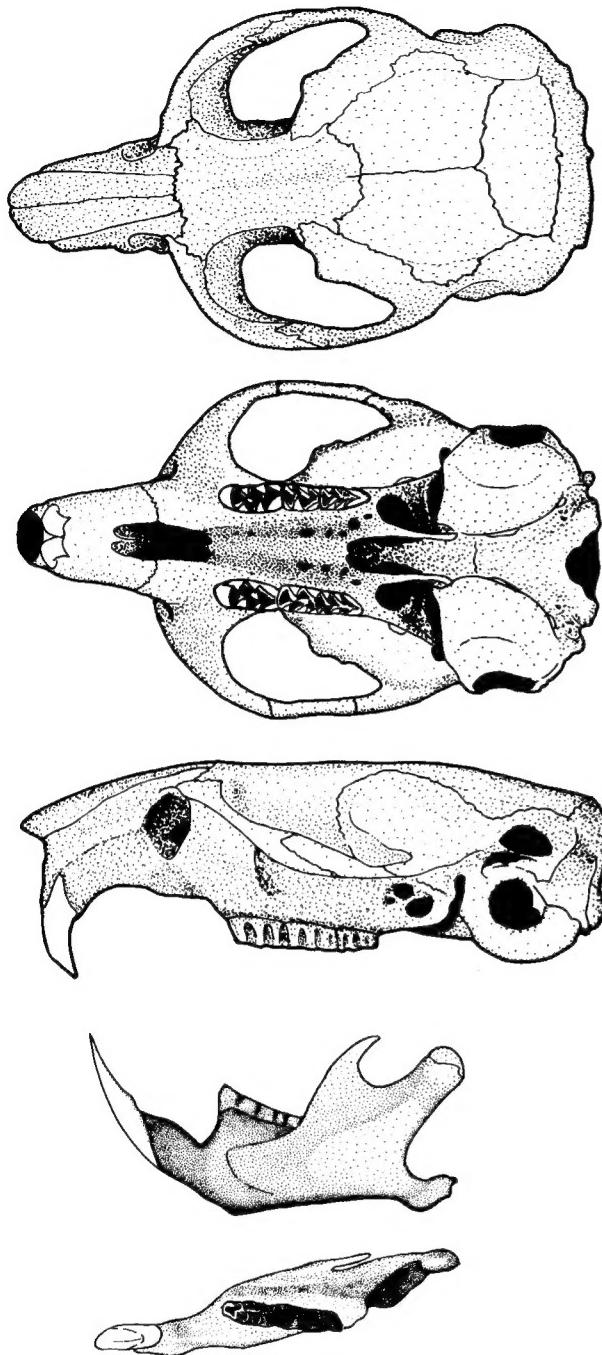


FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral and occlusal views of mandible of female *Phenacomys intermedius* from Delta Co., Colorado (KU 60049). Occipitonasal length of skull is 23.6 mm.

listed nine biogeographic provinces in which *P. intermedius* occurred: East and West Hudsonian, East and West Canadian, Montanian, Coloradan, Oregonian, Sierran, and Columbian. However, inspection of his map indicates that the species also occurs in the Yukonian, Vancouverian and Humboldtian provinces.

FOSSIL RECORD. The fossil record of *Phenacomys* extends to the middle Pleistocene (Irvingtonian) in most of North America (Martin et al., 1986), and to the Pliocene in Beringia (Reprenning et al., 1987). *Phenacomys intermedius* currently is restricted to boreal habitats; thus it is considered to be a good indicator of past climates. All fossil specimens of *P. intermedius* known to Guilday and Parmalee (1972) were individual molars or tooth rows. Identification to species is difficult; the variability within the species is large enough to mask specific differences. Guilday and Parmalee



FIG. 2. Juvenile heather vole, *Phenacomys intermedius*. Photograph from a slide by Murray L. Johnson.

(1972) referred all fossils to *P. intermedius* based on environmental analogy. These Pleistocene finds extended to Kansan time, and ranged as far south as northern Arkansas and Tennessee (Parmalee and Klippel, 1981; Semken, 1984), well south of the present range of the species (Fig. 3).

During the Pleistocene, boreal habitats and climates were widespread over the Great Basin and the biota dispersed over the area (Wells, 1983). When climatic conditions change in the Holocene, the only boreal habitat available was restricted to mountainous "islands" with inhospitable habitat in the lowlands, preventing dispersal of boreal-adapted mammals such as *Phenacomys* (Brown, 1971, 1978). As the boreal islands receded, the range of *Phenacomys* contracted, and it eventually became extinct in the Great Basin ranges. The presence of a mid-Holocene record of *P. intermedius* at Gatecliff Shelter in central Nevada was considered by Grayson (1981) as support for Brown's hypothesis.

Mead et al. (1982) and Thompson and Mead (1982) described a second, late Pleistocene (Wisconsinan) *Phenacomys* locality from Smith Creek Cave in the Snake Range of Nevada. They also supported the relic hypothesis of the boreal-mammal diversity in the Great Basin, but their floral data suggested that the boreal habitats may not have attained a continuous distribution, as previously thought; instead the intervening lowland habitat may have acted as a filter bridge that allowed selected mammals with the ability to migrate across it access to the boreal island habitats. Miller (1976) identified four *Phenacomys* molars from the Silver Creek Local Fauna, Summit Co., Utah. The environment was considered to be a marshy area surrounded by patches of grassland during Late Sangamon or Early Wisconsinan age.

Additional Midwestern Pleistocene records include: Hall Ash Local Fauna, Jewell Co., Kansas (Eshelman and Hager, 1984); Trapshoot Local Fauna, Rooks Co., and Coon Creek Local Biota, Graham Co., Kansas (Martin et al., 1986); Uptegrove Quarry, Cheyenne Co., Nebraska (Voorhies, 1984); Smith Falls Local Fauna, Cherry and Brown Cos., Nebraska (Voorhies and Corner, 1985); Litchfield Local Fauna, Sherman Co., Nebraska (Martin et al., 1986); Craigmire and Waubonsie local faunas, Mills Co., Iowa (Rhodes, 1984); and Java Local Fauna, Walworth Co., South Dakota (Martin, 1973). Voorhies (1984) assigned *Propriophenacomys uptegrovensis* of reputed Miocene (Kimballian) age to *Phenacomys intermedius*, considering it to be an intrusive of Late Pleistocene or Early Holocene age.

The first *Phenacomys* specimens from sites in the East Beringian refugium west of the continental ice sheets were found along the Old Crow River (Jopling et al., 1981; Morlan, 1984) and are of Olduvai age (1.67–1.89 my; C. A. Reprenning, personal communication).

Earlier records of *Phenacomys*, all assigned to extinct species, are restricted to Beringia. Guthrie and Matthews (1972) named "*Pliomys*" *deerlingensis* from the Cape Deceit Fauna (dated about 2.1 my) of the Seward Peninsula, Alaska, but Chaline (1975) demonstrated that it was a species of *Phenacomys*, and the genus was later reported from eastern Siberia (Sher et al., 1977). Finally, Reprenning et al. (1987) described a new species, *Phenacomys gryci*, from the Fish Creek Fauna on the Arctic Ocean coast of northern Alaska that is significantly more primitive than *P. deerlingensis*. They dated this fauna at about 2.4 my, and speculated that *Phen-*

nacomys was derived from Palearctic *Cromeromys* about 4 mya; Martin et al. (1986) also subscribed to an Asian origin for *Phenacomys*.

FORM AND FUNCTION. Hall (1981) listed ranges of external body measurements (in mm) as: total length, 130 to 153; tail length, 26 to 41; hind foot length, 16 to 18.2; ear length from notch, 11 to 17; and body mass to 40.0 g. These measurements are close to those of Peterson (1966) and Banfield (1974) for *P. i. ungava*. Ranges of selected cranial measurements (in mm) are: condylobasal length, 22.3 to 25.4; length of nasals, 7.1 to 8.6; alveolar length of upper molar row, 5.6 to 6.8; zygomatic breadth, 13.2 to 15.7; lambdoidal breadth, 10.9 to 11.7; least interorbital breadth, 3.0 to 3.9 (Armstrong, 1972; Durrant, 1952; Howell, 1926; Youngman, 1975).

The glans penis is slender and straight-sided, about 3.7 mm long and 2.0 mm in diameter (Hooper and Hart, 1962). The mounds on the baculum are not prominent. The smooth, double-peaked edge of the dorsal lobe is flanked laterally by one or two spine-tipped papillae; the remainder of the crater rim is crenate. The urethral process ends distally in four blunt, subequal lobes. The baculum is straight and slender, with a relatively unexpanded base that is notched rather than pointed medially. On the distal end are one medial and two lateral "digits," as in most arvicolid rodents with a "complex" penis (Vorontsov, 1982). The digits curve ventrally; the medial tapers from base to tip, whereas the laterals are laterally compressed distally. Total length of the baculum is about 3.1 mm; the medial digit is about 0.9 mm and the lateral are about 0.8 mm.

The upper eyelid of *P. intermedius* possesses 12 to 13 ($\bar{X} = 12.7$) tarsal (Meibomian) glands; whereas the lower has 9 to 13 ($\bar{X} = 11.0$), a high number for arvicolid rodents and comparable to the number in lemmings (Quay, 1954a). The diastemal palate exhibits a slender anterior longitudinal ridge similar to that in *Clethrionomys*, but longer, and the inflexi of the upper lips are more extensive, covering the incisive papillae. The first transverse palatine ridge is narrow, but the last two are broad (Quay, 1954b). The anterior palatine (incisive) foramina are relatively large and anterior in position, but the nasopalatine canal is posterior (Quay, 1954b). Well-developed hip glands are present in adult males (Howell, 1926). The auditory bullae are "small, globular, simple, and without internal spongy tissue; the stapedial artery is naked as it approaches the stapes" (Hinton, 1926:51).

In *P. intermedius* the superficial masseter has a medial insertion on the mandible, and the deep lateral masseter is divided (Kesner, 1980). The superficial temporalis and deep lateral temporalis muscles are small and less distinct than in many other arvicolid rodents, and more similar to the condition in cricetids. A cricetid-like condition also is seen in the internal pterygoid, which has a reduced aponeurosis (that is, loss of bipinnate origin of lateral part) and in the digastric, where a distinct medial portion of the posterior belly is absent.

ONTOGENY AND REPRODUCTION. Innes and Millar (1982) documented breeding in captive western heather voles, *P. i. levis*, and Foster (1961) studied captive eastern *P. i. ungava*. *Phenacomys intermedius* is a seasonally polyestrous breeder (Vaughan, 1969). The breeding season is from May to August, with high-elevation populations possibly having shorter seasons. Females theoretically could produce four litters per season, but a maximum of only three litters per season was reported by Innes and Millar (1982) in Alberta. Gestation requires 19 to 24 days (Foster, 1961; Innes and Millar, 1982); mean litter size is 4.41 for overwintered females and 3.62 for young-of-the-year females, a statistically significant difference (Innes and Millar, 1982). Other reports (Anderson, 1959; Pruitt, 1954; Williams, 1952) suggest larger litter sizes in wild-caught heather voles farther south, in Colorado. Here three adult females each had seven embryos, one young-of-the-year had four, and one of uncertain age, five (\bar{X} all ages, 6.0). Vaughan (1969) reported smaller values from Grand Co., Colorado (\bar{X} embryos, 4.8; placental scars, 5.3; combined, 5.2; range, 2 to 9; $n = 15$), but still larger than in the Alberta population. Foster (1961) found mean litter sizes of 5.9 and 3.8 for adult and young-of-the-year, respectively, in eastern heather voles; Harper (1956, 1961) reported similar embryo counts in voles from Kuwaitin and Ungava, and suggested that only two litters per year were born. In Colorado, females become sexually mature and breed at about 4 to 6 weeks of age, so females born early in the summer may breed that season, but those born later mature the following spring; males do not become sexually mature during their first summer but breed the next year

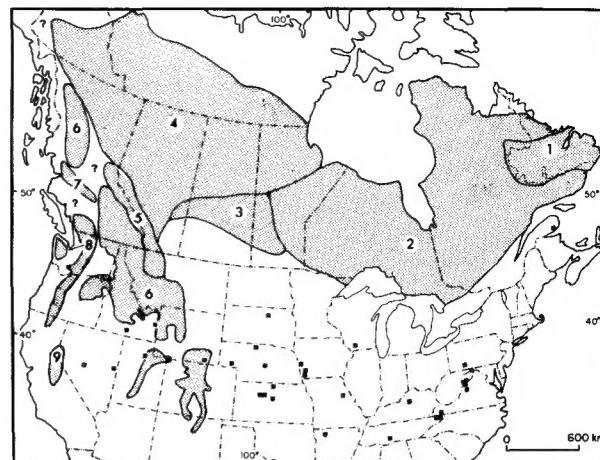


FIG. 3. Geographic distribution of *Phenacomys intermedius*, based on Hall (1981); modified according to Armstrong (1972), Cowan and Guiget (1956), Long (1965), and Maser and Storm (1970). 1, *P. i. crassus*; 2, *P. i. ungava*; 3, *P. i. soperi*; 4, *P. i. mackenii*; 5, *P. i. levis*; 6, *P. i. intermedius*; 7, *P. i. laingi*; 8, *P. i. oramontis*; 9, *P. i. celsus*. Hall (1981) listed *P. i. intermedius*, rather than *P. i. oramontis*, from the Cascade Mountains of southern Oregon and northern California. Question marks indicate areas from which no specimen records are available, but that may prove to be occupied. Pleistocene records referred to in the text are indicated by solid squares, as is a record from Quebec (LaSalle, 1984).

(Vaughan, 1969). However, Innes and Millar (1982) reported that both sexes mature in the year of their birth.

The mean weight of neonates in western *Phenacomys* was 1.89 g and mean weight of litters, 7.99 g (Innes and Millar, 1982). Foster (1961) recorded a mean mass of 2.4 g and mean crown-rump length of 3.0 cm for neonates in eastern *P. i. ungava*. The young were altricial at birth, pink, wrinkled, hairless, and blind. By the end of the first day the dorsum showed pigmentation and the mystacial vibrissae had become barely visible. They vocalized by the 2nd day and could right themselves by the 6th day. On the 8th day they crawled and on the 9th scrambled with fair coordination. This was also the time when the lower incisors could first be seen clearly. They walked by the 12th day and began to leave the nest by the 13th. The eyes also opened on the 13th and they began to eat solid foods by this time although suckling possibly continued until the 19th day. Adult weight (27 g) was attained in about 100 days.

Halfpenny and Ingraham (1983) followed early growth and development in captive western *P. i. intermedius* from alpine tundra habitat in the Front Range of Colorado. Four litters of four to six siblings were studied and growth data for the first 21 days were fitted to the regression line $Y = 1.17 + 0.62X$ ($n = 356$, $r = 0.97$). The mean geometric growth constant calculated from birth to 28 days was 0.079 ($n = 9$). Mean weight gain per day was 0.82 g for the first 21 days. The sequence of developmental characters was in days since birth: pinnae unfold, 3.7; lower incisors erupt, 7.0; front crawl, 11.4; scramble, 13.1; eyes open, 14.6; walk, 15.9.

Halfpenny and Ingraham (1983) noted that Colorado *P. i. intermedius* had a slower rate of development but larger adult weight and faster growth than *P. i. ungava*. They suggested that the differences in Colorado *Phenacomys* were an adaptation to a shorter summer season in the alpine tundra. Moreover, the growth rate of *P. i. levis* from 2,240 m in the Alberta Rockies was even slower, with $Y = 0.79 + 0.43X$ ($n = 240$, $r = 0.97$); no data on development were published by Innes and Millar (1982) except eye-opening, which at 15.5 days was later than in the Colorado population.

Foster and Peterson (1961) found that length of the molar row and rostrum increased with age in captive-reared *P. i. ungava*, and employed this to determine the age of wild-caught animals. They estimated that wild *Phenacomys* had a maximum life span of 4 years or less based on the amount of tooth wear seen in specimens in their third summer.

ECOLOGY. Although found primarily in coniferous forest biomes, *P. intermedius* occurs in a wide range of habitats from moist to xeric (Negus, 1950; Williams, 1952, 1955). Typical habitat

(Banfield, 1974:193) is "dry, open coniferous forest . . . with an understory of heaths such as blueberry, sheep laurel, dwarf birch, and soapberry. . . . Another favourite habitat seems to be shrubby vegetation on the borders of forests and in moist, mossy meadows." A survey of published records by Edwards (1955) tabulated western vole habitats as follows: 54% dry; 72% dry, but in proximity to surface water; and 64% in successional vegetation. Heather-like vegetation is a common element in *Phenacomys* habitats.

Foster (1956, 1961) summarized habitats of eastern *Phenacomys i. ungava*. Approximately 80% of the published habitat descriptions were dry, and of these 29% were dry with proximity to open water; wet habitats accounted for the remaining 20%. Vegetation was listed as 40% spruce (*Picea*), pine (*Pinus*) or pine and spruce combined, "15% mention sagebrush, *Vaccinium* or other members of the Ericaceae, while grass, poplar, willow, brush, sphagnum, etc. are only minor in the list" (Foster, 1961:190). He also mentioned that tree-line is a common descriptor of the habitat but thought this might be because of the narrowness of the boreal habitat on many mountain slopes. Although they use open habitats, some structure in the environment is sought. Brush heaps were mentioned in 16% of the descriptions and shelters such as stumps, logs, hummocks, brush, and frost cracks in tundra are considered favorable. Foster (1961) found that captive *Phenacomys* selected cages with cover, especially edible cover. A dense low-shrub layer may, by providing visual screening and spatial barriers, reduce intraspecific interference and promote higher population density (Naylor et al., 1985). Tundra with no shelter or pure grassy areas did not seem to harbor *P. i. ungava*, although Harper (1961:71) found them "among rocks . . . above timberline" in Quebec.

Western heather voles regularly occur at and above timberline (Brown, 1967; Findley and Negus, 1953; Negus and Findley, 1959; Pattie and Verbeek, 1967). In alpine communities on the Beartooth Plateau, Wyoming, they are common in krummholz, of regular occurrence in moist alpine meadow, and scarce in dry meadow, fellfield, rock-polygons, and talus. They were not found in wet-sedge tussock or willow-sedge communities (Hoffmann, 1974). Reichel (1984) found them to be the most common arvicolid rodent in alpine areas of the Pacific Northwest, where they exhibited a statistically significant association with krummholz and wet (= moist) meadows (Reichel, 1986); he also claimed that willows were used, but his data (Reichel, 1986, Table 1) do not support this. Microhabitat use was influenced by rock cover; 10 to 25% coverage of a mixture of medium (11 to 150 cm) and large (>150 cm) rocks was used rather than uniform-sized rocks, or greater or lesser coverage (Reichel, 1986). Slope and aspect did not influence microhabitat use.

To characterize small mammal communities, Nagorsen and Peterson (1981) divided Quetico Provincial Park in Ontario, Canada, into five habitats and found that *P. intermedius* was most abundant in the upland conifer and upland mixed forests. Lowland conifer and wet meadow had sparse representation whereas lowland mixed forest yielded no *Phenacomys*. They concluded that differences in species abundance and diversity were a reflection of vegetation and available food resources, but did not detail floristic data. Also in Ontario, Naylor and Bendell (1983) found that in jack pine (*Pinus banksiana*) forests, *P. intermedius* was most abundant in pure stands of medium age with nearly continuous ericaceous ground cover.

Krebs and Wingate (1976, 1985) trapped *P. intermedius* in 10 of 21 possible habitats over a 5-year period in the Kluane Lake region of southwestern Yukon Territory. In decreasing order of relative abundance (based on 100 trap nights) these were: willow (*Salix glauca*); balsam poplar (*Populus balsamifera*); shrub birch (*Betula glandulosa*)-meadow (*Festuca altaica*); open spruce (*Picea glauca*)-willow; aspen (*Populus tremuloides*); open spruce-buffaloberry (*Shepherdia canadensis*); closed spruce; closed spruce-buffaloberry; open spruce-birch; closed spruce-willow (Krebs and Wingate, 1976). In contrast, Millar et al. (1985) found *P. intermedius* in the Kananaskis Valley, Alberta, to be most abundant in deciduous and coniferous riparian forest habitats, open spruce (*Picea engelmannii*) forest, alpine larch (*Larix lyallii*), and subalpine meadows. Of 12 habitats sampled, *Phenacomys* was not trapped in closed pine or spruce-fir forest, and occurred with variable frequency in aspen, open pine, spruce, or larch (*Larix*), and alpine meadow or talus. The niche-breadth index for *Phenacomys* was 0.64, smaller than that of sympatric *Peromyscus maniculatus* (0.77), but larger than *Microtus longicaudus* (0.60), *Clethrionomys gapperi* (0.53), and *M. pennsylvanicus* (0.37). The Kananaskis Valley *Phenacomys* had the widest niche overlap with other species among those sampled;

with *C. gapperi* (0.93) in 1980, with *M. longicaudus* (0.84) in 1981, and with *M. pennsylvanicus* (0.87) in 1982. For all 3 years combined, the widest niche overlap was with *M. longicaudus* (0.86), and the smallest with *P. maniculatus* (0.63), notable because these two species also had the largest niche breadths.

Comparing the Kananaskis Valley data with those from the Kluane Lake region, Millar et al. (1985:203) stated: "*Microtus longicaudus* and *P. intermedius* were most abundant in similar habitats (subalpine meadows vs. subalpine tundra and riparian coniferous vs. willow, respectively) in both areas." However, at Kluane Lake, the niche-breadth index for *Phenacomys* was only 0.24, and for *M. longicaudus*, 0.15; both much lower than at Kananaskis. Moreover, greatest niche overlap was shared with *M. oeconomus* (0.35), *M. longicaudus* (0.29), *M. pennsylvanicus* (0.27), and *P. maniculatus* (0.26), while *C. rutilus* (0.20) and *M. miurus* (0.12) exhibited the least overlap with *Phenacomys*. These niche-overlap values at Kluane Lake (61°N) all are much smaller than those for the same or congeneric species at Kananaskis (51°N), and may reflect the lower primary productivity of the more northerly locality that is close to the northern edge of the range of *Phenacomys*. Moreover, at Kluane Lake, *Phenacomys* occurred in only 10 to 21 habitat types (48%; Krebs and Wingate, 1976), or 5 of 18 (28%; Krebs and Wingate, 1985), when a different classification was used. In contrast, *Phenacomys* at Kananaskis, within the heart of the coniferous forest distribution of the species, occurred in 12 of 14 (86%) habitat types sampled (Millar et al., 1985). This suggests that at the edge of their range, *Phenacomys* may be restricted to the most favorable habitats, thus exhibiting both reduced niche breadth and less overlap with other sympatric species.

Catch per 100 trap nights with Museum Special traps baited with peanut butter for *P. intermedius* at Kluane Lake, Yukon, from 1973 to 1977 ranged from 0.03 to 0.18 ($\bar{X} = 0.10$) for all habitats (Krebs and Wingate, 1985). In the Kananaskis Valley, Alberta, during 1980, 1981, and 1982, Millar et al. (1985) with similar traps baited with peanut butter and oats found a range of from 0.24 to 0.70 ($\bar{X} = 0.48$) for all habitats, suggesting that western *Phenacomys* has a higher relative abundance in more southerly communities. Naylor et al. (1985) found indices in jack pine (*Pinus banksiana*) forests in Ontario ranged from 0.15 to 9.59 ($\bar{X} = 2.09$). Pure stands have higher relative densities ($\bar{X} = 4.04$); and those of medium age (40 years) supported more *Phenacomys* than young (20 years) or old (60 years) stands. In recently disturbed forests, the index was 0.30 to 0.86 ($\bar{X} = 0.58$), less than had been reported for other clear-cut stands in Ontario (1.3–3.6; Martell, 1983; Martell and Radvanyi, 1977). Mixed stands of jack pine, black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and aspen yielded the lowest indices (0.0 to 0.15, $\bar{X} = 0.10$). Most *Phenacomys* caught in mixed stands were juveniles; such habitats may act as dispersal sinks (Naylor et al., 1985). The only absolute estimates of density of heather vole populations were 10/ha for alpine communities of the Beartooth Plateau (Hoffmann, 1974) and 0.5 to 4.3/ha for montane forest (Innes and Millar, 1982).

In food habits, *Phenacomys* is herbivorous. Shaw (1924) noted denuded twigs of white heather (*Cassiope* sp.) and beargrass (*Xerophyllum* sp.) that had been used for food near nests of western *P. i. oramontis*. Winter foods of *P. i. ungava* include bark of bush willow (*Salix* sp.), dwarf birch (*Betula glandulosa*), sheep laurel (*Kalmia angustilolia*) and blueberry (*Vaccinium* sp.; Banfield, 1974; Foster, 1961). In late spring, crushed seeds and lichens were found in the stomachs of five *P. i. ungava* (Foster, 1961). It was suspected that seeds also were eaten in fall when they were abundant. During summer, food caches included foliage and fruits of willow, bearberry (*Arctostaphylos uva-ursi*), blueberry, soapberry (*Shepherdia canadensis*), and dwarf birch depending upon availability. Harper (1956) reported mountain cranberry (*Vaccinium vitis-idaea*) in the mouths of foraging *P. i. mackenzii*. Cowan and Guiget (1956) asserted that bearberry composed 85–90% of the diet of *P. i. intermedius* in British Columbia in both summer and winter, whereas buffaloberry made up 6%, and *Rosa*, *Vaccinium* and others, 5–10%. The hypogeous fungus *Endogone* is eaten occasionally (Williams and Finney, 1964).

Food caches are common in both winter and summer, being collected and left in piles at burrow entrances (Racey, 1936). Naylor et al. (1985) found many caches of sheep laurel at burrow entrances in summer, and noted that cover of this species was the habitat factor most highly correlated with relative abundance of *Phenacomys* in coniferous forest in Ontario ($R^2 = 0.9296$; $P < 0.05$). Caches

seem to be produced in the evening and night when the animals are most active, and probably are eaten during the day in comparative safety.

Phenacomys intermedius has been reported by Douglass and McDonald (1976) in feces of martens (*Martes americana*). The long-tailed weasel (*Mustela frenata*) may be a major predator when it is abundant, although its main prey is *Peromyscus* (Pattie and Verbeek, 1967) or *Microtus* (Quick, 1951). Only one possible sighting (Ingles, 1942) implicates the ermine (*M. erminea*) as a predator of *P. intermedius*. Foster (1961:194) observed eastern *Phenacomys* "in the talons or at the nests" of *Surnia ulula* (hawk-owl) and *Asio flammeus* (short-eared owl). He also assigned *Phenacomys* in raptor pellets, in order of importance, to *A. flammeus*, *Nyctea scandiaca* (snowy owl), *S. ulula*, and *Buteo lagopus* (rough-legged hawk). Many fossil localities probably are deposits of owl pellets (Guilday and Parmalee, 1972). Banfield (1974) stated that *Phenacomys* is not overly cautious and that this could explain its frequent occurrence in owl pellets. The dense ericaceous ground cover typical of heather vole habitats may provide shelter from predators for this unwary vole (Foster, 1961; Naylor et al., 1985). At a time of high population density *Phenacomys* also has been identified in stomachs of speckled trout (*Salvelinus*; Peterson, 1956).

The fleas *Anomiopsyllus* sp., *Oropsylla idahoensis*, and *Thrassis acamantis* were reported from *P. i. intermedius* (Hubbard, 1947). The last two species are primarily fleas of ground squirrels (*Spermophilus* sp.). Kinsella and Pattie (1967) later added *Magabothris abantis* to this list. Foster (1961) reported four species of fleas from *P. i. ungava*: *Magabothris quirini*, *M. groenlandicus*, *Malaraeus penicilliger athabascae*, and *Peromyscopsylla h. hamifer*. The bot fly (*Cuterabra* sp.) also was reported (Foster, 1961). Other ectoparasites include sucking lice (Anoplura, kinds not listed; Jellison, 1942), and *Polyplax abecisa* (Harper, 1956). Harper (1956, 1961) found acarine mites infesting *Phenacomys*, and Kinsella and Pattie (1967) reported two ticks, *Haemogamasus* sp. and *Ixodes sculptus*. Nematodes include *Nematospiroides dubius* from Quebec (Schad, 1954), and several species of *Heligmosomoides*. Durette-Desset et al. (1971) hypothesized that *H. polygyrus americanus* had a dual origin for North American rodents. The first introduction occurred in the Pleistocene, with infected microtine rodents (not including *Phenacomys*) migrating over the Bering land bridge. The second introduction occurred with the recent introduction of *Mus musculus*, from which *Reithrodontomys* and *Phenacomys* became infected. However, the spread of the parasite throughout the geographic range of *Phenacomys* (Rausch and Rausch, 1973) likely did not occur as quickly as postulated by a *Mus* introduction, nor does the occurrence of *H. p. americanus* in isolated populations of *Phenacomys* support this hypothesis. Possibly the nematode was widely distributed in *Phenacomys* before the subspecies were differentiated. Kinsella (1967) reported *H. dubius* in *Phenacomys*, and Rausch and Rausch (1973) also described a new species, *H. johnsoni*, from the caecum of *Phenacomys*. Cestodes found in the heather vole include *Andrya primordialis* from Wyoming and Montana (Kinsella, 1967; Rausch, 1952; Rausch and Schiller, 1949), *A. communis* (= *primordialis*) from Alberta (Lubinsky, 1957), and *A. bairdi* (= *primordialis* ?) and *A. macrocephala* from Quebec (Schad, 1954); the latter two originally were identified as coming from *Microtus chrotorrhinus*, but Peterson (1962) corrected the host identification. Additionally, *Paranoplocephala variabilis* was recorded from *P. i. intermedius* from Alberta (Lubinsky, 1957).

BEHAVIOR. During summer *P. intermedius* occupies short underground burrow systems (Smith and Foster, 1957). The underground nest is constructed of grass, moss, or leaves and is about 10 cm in diameter (Racey, 1936). Nests are not found below 20 cm in depth and often are found immediately under a rock, stump, log, or in a cavity within a decayed log (Cowan and Guiget, 1956). Runways are indistinct and the burrow opening often is overgrown. Winter nests are about 15 cm in diameter and are constructed of leaves, grass and twigs; they are lined with shredded snowgrass (*Juncoides* sp.) or other graminoids and sealed against snow with branching lichens (Shaw, 1924). These subnivian nests are located on the ground surface, at the base of a willow bush, stump, or rock. Defecation appears to be restricted to "latrines" on the surface adjacent to runways or burrows; the feces have a characteristic aromatic odor (Smith and Foster, 1957).

Phenacomys intermedius is mild tempered and docile when captured (Smith and Foster, 1957). During the breeding season,

captive males are aggressive to other males; females with young are aggressive to any intruders and rear their young alone (Foster, 1961). Banfield (1974) stated that family groups huddle together in communal nests in winter. Harper (1961) observed that a captive adult (sex undetermined) was subordinate to a subadult *Clethrionomys gapperi* caged with it.

In captivity, *P. intermedius* does not eat commercial laboratory chow readily (Foster, 1961; Innes and Millar, 1982), and even if supplied with palatable foods, exhibits high mortality, especially among infants (Halfpenny and Ingraham, 1983; Innes and Millar, 1982).

The heather vole has a reputation for being widely but sparsely distributed; low efficiency of snap traps relative to pitfall traps may be responsible (Edwards, 1952), but Naylor et al. (1985) found the reverse to be true. Douglass and McDonald (1976) in 70,000 trap nights at Chick Lake captured one *Phenacomys*, but teeth of *P. intermedius* occurred in 5% of the marten feces in the area. Innes and Millar (1982) noted, besides low trappability, high mortality in live traps (35%). Although the animals ate the bait (carrots and whole oats) they did not use the nesting material provided to prevent hypothermia. Sex ratios of captive-born litters were not statistically different from 1:1, but females were more likely to be caught than males by a ratio of 3:1 (Innes and Millar, 1982) or 1.4:1 (Naylor et al., 1985); female recaptures also were more frequent. Innes and Millar (1982) suggested that males in some way avoid traps, and do not occupy different habitats (Saunders, 1927), and their sex ratios are not skewed toward females (Taylor, 1915).

Foster (1961) found eastern *Phenacomys* to be more active during twilight and night rather than the day. He also noted low trappability and considered that snap traps set in lines may not be as efficient as either pitfall traps, or trapping directly in front of burrow holes.

Although trapping usually produces few specimens, occasional population "explosions" have resulted in an increase in number of trapped specimens (Foster, 1961; Naylor et al., 1985; Peterson, 1956; Smith and Foster, 1957).

GENETICS. The karyotype of *P. intermedius* (including both *P. i. ungava* and *P. intermedius*) exhibits a diploid number of 56. The fundamental number of autosomal arms is 54 to 56, there being a single pair of small submetacentric chromosomes, at least in *P. i. intermedius*. The X chromosome is submetacentric, and the Y is a small acrocentric, comparable in size to the smallest acrocentric autosomal pair (Hsu and Benirschke, 1971; Matthey, 1957). Matthey (1957) considered this chromosomal complement to be close to the primitive, entirely acrocentric, arvicolid karyotype ($2n = 56$, FN = 56) that also is found in other morphologically primitive genera including *Prometheomys*, *Dinaromys*, *Alticola*, *Eothenomys*, *Clethrionomys*, and *Eolagurus* (Orlov and Bulatova, 1983).

REMARKS. Hall and Cockrum (1953) employed the subspecific name combination *P. i. celatus*, with *latimanus* and *ungava* as synonyms, invoking page priority in anticipation of formal approval of proposed changes in the International Rules of Zoological Nomenclature (Handley, 1954). However, Article 24a of the International Code of Zoological Nomenclature (Stoll et al., 1961:25) provided that in the case of simultaneous publication, "relative priority is determined by the action of the first reviser." Miller (1897) selected *ungava* in preference to *celatus*, and was followed by Howell (1926) and virtually all subsequent authors except Hall.

Hall (1981:785) also commented that *P. intermedius* "may be a composite of two and three allopatric species," apparently alluding to *ungava* and *mackenzii* that previously had been considered specifically distinct from *intermedius*. Anderson (1942) arranged *mackenzii* as a subspecies of *P. ungava*, but Crowe (1943) claimed evidence of intergradation between *P. intermedius levis* and *P. "ungava" mackenzii*, and united all taxa in *P. intermedius*. This was disputed by Foster and Peterson (1961) and Peterson (1966), who continued to maintain *P. ungava* as a distinct species. In this review, we have referred to populations assigned to *ungava* as "eastern," and to *intermedius* as "western" heather vole.

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